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Impact of Heat Stress on Meat, Egg Quality, Immunity and Fertility in Poultry and Nutritional Factors That Overcome These Effects: A Review

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Abstract: Modern strains of poultry have been produced to meet the demands of consumers in terms of quantity and they are affected by problems associated with immunity (sensitivity to infection with different diseases), stressors (high sensitivity to different stressors) and product quality (meat and egg quality). In particular, heat stress (HS) negatively affects the productive performance, meat yield, egg yield, meat quality (visual appearance and chemical characteristics), egg quality (internal and external), reproductive performance, intestinal functions and immune response. In addition, there is increased awareness among consumers of the quality of food and the industry must aim to satisfy the higher requirements of consumers. Thus, there is increased pressure on poultry producers to improve their production quantity and quality. As a consequence, it is important to know how HS affects the meat quality, egg quality, immune organs, intestinal functions and reproductive organs in order to protect against any negative effects. In addition, it is essential to determine the roles of nutritional factors and the possibility of using them to overcome the negative effects of HS. This review summarizes current research in these areas.

Key words: Heat stress, product quality, nutritional factors, poultry

INTRODUCTION

The productive performance and meat yield of modern meat-type chicken strains as well as egg production by egg-type chickens have been enhanced by selection processes to satisfy the needs of consumers (Havenstein *et al*., 2003; Flock *et al*., 2005; Silversides *et al*., 2006). However, these improvements have been accompanied by some problems in meat-type birds, including pale, soft, exudative meat and low resistance to diseases (Petracci *et al*., 2015; Cheema *et al*., 2003; Cheng *et al*., 2013; Pohjola *et al*., 2015). In meat-type birds, meat color and drip loss are among the most important visual traits in terms of meat quality that motivate consumers to accept or reject meat (Fletcher, 2002), while in egg-type birds, low eggshell quality can lead to a high percentage of broken and cracked eggs and thus huge economic losses (Etches, 1996; Perez-Huerta and Dauphin, 2016). The global climate has changed (Smith and Gregory, 2013) so tropical and subtropical areas will be affected more frequently by high ambient temperature, especially traditional farms that depend on natural ventilation. Heat stress (HS) can decrease the feed intake, body weight gain and feed efficiency (productive performance) (Bonnet *et al*., 1997; Sahin *et al*., 2003a; Onderci *et al*., 2004; Azad *et al*., 2010a; Habibian *et al*., 2016), meat yield (Temim *et al*., 2000; Onderci *et al*., 2004; Lu *et al*., 2007; Zhang *et al*., 2012a,b; Zeferino *et al*., 2013, 2016) and egg yield (Mashaly *et al*., 2004; Franco-Jimenez *et al*., 2007; Sahin *et al*., 2008a,b; Ma *et al*., 2014; Akdemir *et al*., 2015); as well as affecting the meat color, juiciness and taste (Feng *et al*., 2008; Wang *et al*., 2009; Hao and Gu, 2014), and internal and external egg quality (Mashaly *et al*., 2004; Ebeid *et al*., 2012; Ma *et al*., 2014); and reducing the secretion of digestive enzymes, absorption of nutrients (Hai *et al*., 2000; Liu *et al*., 2016), proportions of immune organs (Bartlett and Smith, 2003; Niu *et al*., 2009a-c; Liu *et al*., 2014; Jahanian and Rasouli, 2015), synthesis of antibodies (Bartlett and Smith, 2003; Mashaly *et al*., 2004; Tang and Chen, 2015), relative weights of reproductive organs (testis, ovary and oviduct) (Rozenboim *et al*., 2007; Chen *et al*., 2015), semen quality (volume, sperm concentration, lifetime sperm number and mobility) (Joshi *et al*., 1980; Turk *et al*., 2015, 2016) and large follicle count in poultry (Rozenboim *et al*., 2007). In this review, we discuss the negative effects of HS on the poultry industry (Fig. 1-3) and the roles of nutritional factors in overcoming these effects.

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DISCUSSION

Meat quality: In poultry, HS can cause reductions in the carcass, breast and thigh proportions (Temim *et al.*, 2000; Onderci *et al.*, 2004; Sahin *et al.*, 2003b, 2005a,b 2006; Lu *et al.*, 2007; Zhang *et al.*, 2012a,b; Zeferino *et al.*, 2013, 2016), protein deposition and the intramuscular fat percentage in breast muscles (which negatively affects the meat yield, nutritional value and meat taste), as well as increases in the proportion of abdominal fat (which negatively affects the carcass appearance and consumer acceptance) (Baziz *et al.*, 1996; Lu *et al.*, 2007; Zhang *et al.*, 2012a,b; Dai *et al.*, 2009; Zeferino *et al.*, 2016; Habibian *et al.*, 2016). Protein and fat deposition in the breast muscles are decreased in chickens subjected to HS due to depressed protein synthesis and enhanced protein breakdown (Yunianto *et al.*, 1997; Temim *et al.*, 2000) (which leads to a reduction in the diameter of myofibers (Joiner *et al.*, 2014)) and fat breakdown (Mujahid *et al.*, 2007; Azad *et al.*, 2010b; Boussaid-Om Ezzine *et al.*, 2010). In addition, the lightness and drip loss of breast muscle are increased significantly in heat-stressed chickens (Lu *et al.*, 2007), whereas the pH_0 declines significantly, while there are also significant increases in the lightness, drip loss and shear force of breast muscle (Feng *et al.*, 2008); declines in the ultimate pH, pH_{30}, pH_{24} and water-holding capacity and increases in the drip loss and cooking loss of broiler breast muscle (Wang *et al.*, 2009; Hao and Gu, 2014). In chickens, Zhang *et al.* (2012a,b) reported significant declines in the ultimate pH and redness value under HS conditions, as well as the drip loss, cook loss, shear force and lightness value of thigh breast muscles. In heat-stressed turkeys, the pH_0, pH_2, or pH_{24} values were lower, whereas the lightness value, drip loss and cooking loss were higher compared with a control group (thermo neutral temperature) (McKee and Sams, 1997). Exposing quails to HS increases the percentage of drip loss compared with the standard temperature (Remignon *et al.*, 1998). In rabbits, the longissimus muscle lightness and cooking loss are elevated by HS (Zeferino *et al.*, 2013). The high production of lactic acid in the muscles of heat stressed-chickens via glycolysis is considered to be the main reason for the rapid decline in pH (Feng *et al.*, 2008; Zhang *et al.*, 2012a,b; Hao and Gu, 2014), while the generation of excessive amounts of reactive oxygen species (ROS) (superoxide anion radical and hydrogen peroxide) than the body can scavenge leads to the oxidation of sarcoplasmic and myofibrillar proteins (which reduces their solubility and their ability to bind water, thereby leading to increases in drip loss and cooking loss and reducing the water-holding capacity, juiciness and tenderness (Wang *et al.*, 2009)), myglobin protein (which reduces the redness value in the muscles of heat stressed-chickens (Zhang *et al.*, 2012a,b) and lipids (which enhances the production of malondialdehyde (MDA) and reduces the shelf-life of meat (Feng *et al.*, 2008; Wang *et al.*, 2009; Hao and Gu, 2014)). Thus, according to these previous studies, HS leads to rapid declines in the muscle pH and water-holding capacity of poultry, but increases in the lightness value, drip loss and cooking loss. In addition, pale, soft, exudative meat is a major modern problem in poultry meat production, which causes economic losses (Petracci *et al.*, 2015).

However, nutritional factors can have important roles in improving meat production and its quality under HS production conditions, where supplementation with 30 mg zinc (Zn) sulfate plus 4.5 mg vitamin (Vit) A (Kucuk *et al.*, 2003), 250 mg Vit C with 400 mg chromium (Cr) picolinate (Sahin *et al.*, 2003b), 1.0 g ethanol-extracted propolis (Seven *et al.*, 2008), or 5.0 g glutamine plus 0.1 g gamma-aminobutyric acid per kg of diet (Dai *et al.*, 2012) significantly improved the carcass, dressing and breast yield proportions in heat stressed-broiler chickens. Furthermore, supplementation with 30 mg Zn picolinate (Kucuk *et al.*, 2003), 0.6 mg Cr with 2.0 mg biotin (Onderci *et al.*, 2005), 2.0 g magnesium proteinate (Sahin *et al.*, 2005a,b), 400 mg genistein (Onderci *et al.*, 2004), 100 mg lycopene (Sahin *et al.*, 2006), or 250 mg Vit C per kg of diet (Sahin *et al.*, 2003b) improved the carcass yield and dressing proportion in heat-stressed-quails. In heat-stressed rabbits, supplementation with 1.0 g betain/kg diet enhanced the carcass quality, dressing percentage and protein accumulation (Hassan *et al.*, 2011). Supplementing the diet of heat-stressed chickens with 0.4 mg Cr propionate significantly decreased the drip loss and cooking loss (Huang *et al.*, 2016), whereas supplementation with 1.0% glutamine inhibited the rapid decline in the pH, decreased the lightness value and increased the redness value and water-holding capacity of breast muscle (Dai *et al.*, 2009). Moreover, providing HS broiler chickens with 100 mg gamma-aminobutyric acid/kg diet improved the redness value and decreased the lightness value in breast muscles (Dai *et al.*, 2011). All of these studies showed that improvements in the meat yield and quality were accompanied by enhanced growth performance, while supplementation with 200 mg epigallocatechin-3-gallate (Tuzcu *et al.*, 2008), 50 g tomato powder (Sahin *et al.*, 2008a,b), or 200 mg curcumin per kg of diet (Sahin *et al.*, 2012a) improved the productive performance and reduced the MDA content in the meat yield of heat-stressed quails. In broiler chickens, supplementing with 100 mg curcumin (Zhang *et al.*, 2015) or 0.4 g resveratrol per kg diet improved the growth performance (Liu *et al.*, 2014), while adding 1.0 g alfalfa polysaccharides/kg diet improved the growth performance of rabbits under HS conditions (Liu *et al.*, 2010).

Therefore, nutritional factors can improve the growth performance of heat-stressed poultry and they may have

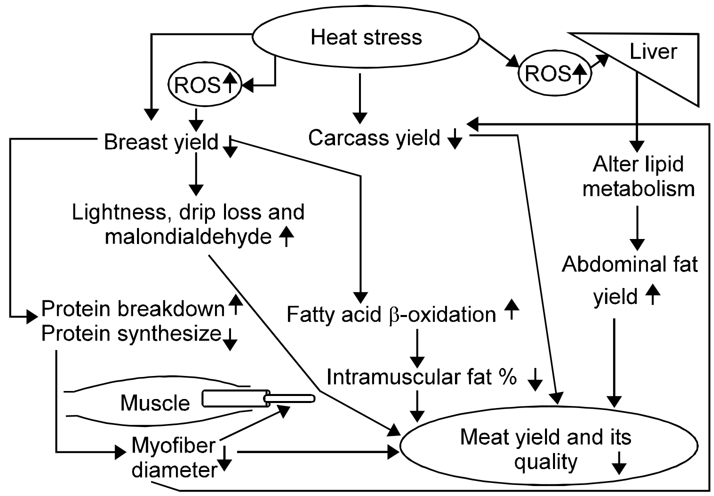

Fig. 1: Effects of heat stress (HS) on the meat yield and quality. High production of reactive oxygen species (ROS) in breast muscles induced by HS may lead to increased lightness by promoting the oxidation of myoglobin, drip loss due to the oxidation of sarcoplasmic and myofibrillar proteins and enhanced malondialdehyde production via increased lipid peroxidation. In addition, HS may reduce the intramuscular fat content due to increased fatty acid β-oxidation and the myofiber diameter may decline due to increased protein breakdown and the inhibition of protein synthesis. High production of ROS in the liver may affect lipid metabolism to increase the abdominal fat yield, thereby reducing the meat yield and quality. ↑, increased: ↓, decreased

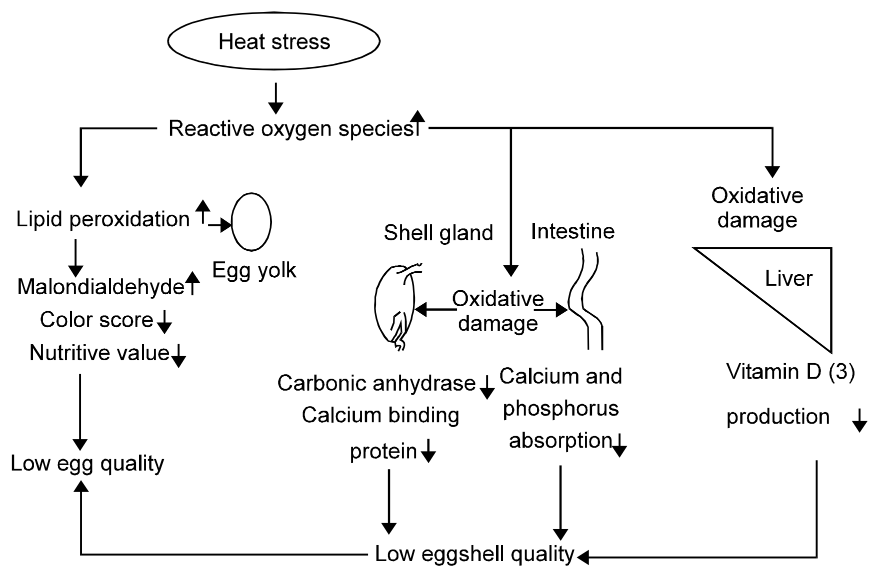

Fig. 2: Effects of heat stress (HS) on egg quality. High production of reactive oxygen species induced by HS may suppress the absorption of calcium and phosphorus, decrease vitamin D production (3) and reduce the secretion of carbonic anhydrase and calcium-binding protein due to the induction of oxidative damage in the intestine, liver and shell gland. In addition, HS may increase the malondialdehyde level as well as reducing the yolk color score and egg nutritional value by enhancing yolk lipid peroxidation, thereby yielding low quality eggs. ↑, increased: ↓, decreased

antioxidant properties that affect the meat quality. In addition, although previous studies have successfully improved meat production and the meat quality of poultry under HS conditions using nutritional factors, they did not fully elucidate the mechanisms that allow nutritional factors to enhance the carcass characteristics and meat quality. Thus, considering how HS negatively affects the carcass characteristics and meat quality of poultry (Fig. 1) as well as the effects of nutritional factors on enhancing the carcass characteristics and meat quality

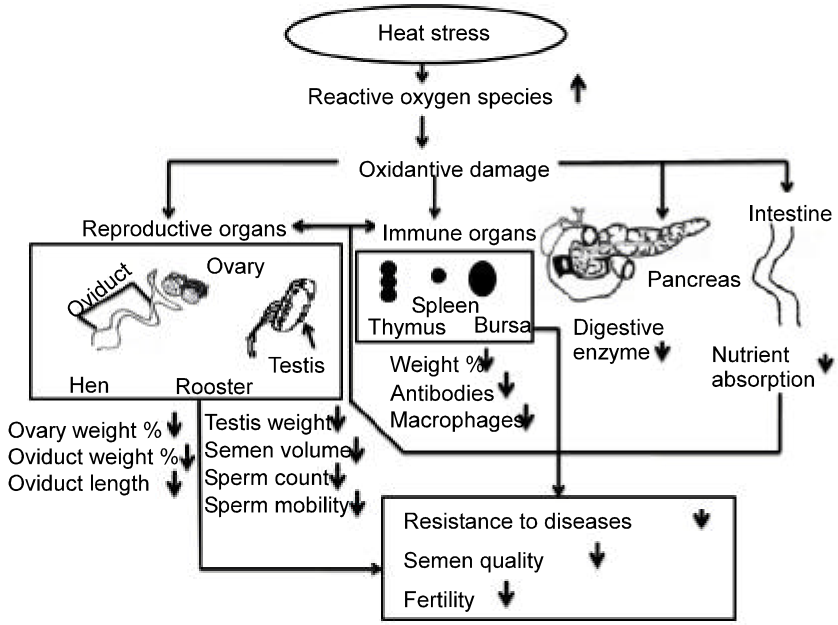

Fig. 3: Effects of heat stress (HS) on immunity, semen quality and fertility. High production of reactive oxygen species induced by HS may reduce the secretion of digestive enzymes and the absorption of nutrients due to oxidative damage induced in the pancreas and intestine, thereby retarding the development of the immune system and reproductive organs. In addition, HS may increase lipid peroxidation of the cell membranes in immune and reproductive organs, thereby impairing their functions. ↑, increased: ↓, decreased

under HS conditions may help to increase our current understanding of the mechanisms that allow nutritional factors to obtain improvements in poultry, there by facilitating future research.

Egg quality: Consumers prefer fresh eggs according to their characteristic features (albumen and yolk appearance and air cell volume), which can be confirmed by evaluating the Haugh unit score, yolk color and MDA content. In addition to these traits, producers are increasingly aiming to produce eggs with a normal egg shape, eggshell thickness and eggshell breaking strength, thereby facilitating the delivery of fresh eggs to consumers. In laying hens, quails and ducks, HS negatively affects the characteristic economic traits related to egg quality, including the Haugh unit score, yolk color, eggshell thickness, percentage breakage rate, nutritional value and shelf life by promoting yolk lipid peroxidation, which leads to high detectable levels of MDA that are associated with low nutritional value and an unfavorable taste (Mashaly *et al.*, 2004; Franco-Jimenez *et al.*, 2007; Sahin *et al.*, 2008a,b; Ebeid *et al.*, 2012; Ma *et al.*, 2014). MDA is also considered to be a toxic compound with detrimental effects on human health due its links with several diseases (Fujioka and Shibamoto, 2004).

Panting is a normal response in heat-stressed birds, which reduces the HCO_3^- and CO_2 levels in the blood, thereby elevating the blood pH and inducing respiratory alkalosis (Franco-Jimenez *et al.*, 2007; Ma *et al.*, 2014). The elevated blood pH and respiratory alkalosis reduce the levels of Ca^{2+}, which is the only form that can be used by the eggshell gland to produce eggshell (Franco-Jimenez *et al.*, 2007; Ma *et al.*, 2014). In addition, decreases in calcium uptake and the presence of abnormal duodenum, jejunum and shell gland epithelial cells appear to be attributable to HS (Franco-Jimenez *et al.*, 2007; Ma *et al.*, 2014; Santos *et al.*, 2015). Moreover, HS reduces the mRNA expression level of carbonic anhydrase and calcium-binding protein in the shell gland (Ebeid *et al.*, 2012; Ma *et al.*, 2014). These changes may explain why HS leads to poor eggshell quality and a high percentage of broken eggs.

Nutritional factors play a vital role in alleviating HS in laying birds. In heat stressed-quails, adding 1.2 mg Cr picolinate (Sahin *et al.*, 2001a, 2002a) or 0.8 mg Cr histidinate per kg of diet improved the eggshell thickness and Haugh unit score, but reduced the egg yolk MDA levels (Akdemir *et al.*, 2015) by enhancing the concentrations of Vit C and E (natural antioxidants), which decreases oxidative damage by suppressing lipid peroxidation (Sahin *et al.*, 2005b). This explains the improved Haugh unit score and the reduced egg yolk MDA level, but the improved eggshell thickness due to the effects of Vit C and E is discussed subsequently in our consideration of eggshell quality. Supplementation with 60 mg Zn sulfate/kg diet improved the eggshell thickness and Haugh unit score in quails under HS conditions (Sahin and Kucuk, 2003). This is because Zn is a component of several enzymes such as carbonic anhydrase, which regulates carbonate ion production during eggshell formation (El-Husseiny *et al*., 2008) and Cu/Zn superoxide dismutase, which increases the antioxidant capacity and decreases lipid peroxidation (Liu *et al*., 2015). Moreover, dietary supplementation with Zn increases the availability of other antioxidants such as Vit C and E (Sahin and Kucuk, 2003; Sahin *et al*., 2005c). Thus, dietary supplementation with Zn can enhance the Haugh unit score directly via its effects as an antioxidant and indirectly by enhancing the concentrations of Vit E and C. Supplementing the diet of heat-stressed quails with 4.0 mg Diachrome, a commercial product that contains chromium picolinate and biotin as active components (Sahin *et al*., 2004), increased the Haugh unit score via the same mechanism as Zn but involving Cr because previous studies detected no significant effects of biotin on antioxidant defense systems (Sahin *et al*., 2005b). Supplementation with 1.0 g arginine silicate inositol/kg diet improved the eggshell thickness and Haugh unit score (Onderci *et al*., 2006) because the arginine metabolites proline and polyamine are involved in collagen production (Fouad *et al*., 2012). Collagen is essential for the initial phase of eggshell calcification (Hincke *et al*., 2012) and silicon participates in eggshell calcification (Rabon *et al*., 1995). In addition, arginine and its metabolites (nitric oxide) have antioxidant properties. Thus dietary supplementation with L-arginine enhanced the antioxidant ability and inhibited lipid peroxidation in quails, broiler breeders and their offspring (Atakisi *et al*., 2009; Duan *et al*., 2015), which may explain why dietary supplementation with arginine silicate inositol improves the Haugh unit score. In heat-stressed quails, dietary supplementation with 800 mg soy isoflavones/kg diet improved the Haugh unit score and eggshell thickness by enhancing the uptake of calcium and phosphorus and thus their availability for eggshell formation (Sahin *et al*., 2007), as well as obtaining direct improvements via its ability to remove free radicals, or indirect changes by increasing the availability of other antioxidants such as Vit E (Akdemir and Sahin, 2009). Moreover, in heat-stressed quails, supplementation with 0.3 mg selenomethionine enhanced the Haugh unit score and reduced the egg yolk MDA content (Sahin *et al*., 2008a,b) by suppressing lipid peroxidation via enhanced glutathione peroxidase (Mahmoud and Edens, 2003).

In heat-stressed hens, supplementation with 200 or 250 mg Vit C per kg of diet (Seven, 2008; Panda *et al*., 2008) enhanced the egg shell thickness, eggshell strength and yolk color (Torki *et al*., 2014), while adding 200 mg Vit C with 250 mg Vit E per kg of diet improved the egg shell thickness in heat stressed-broiler breeders (Chung *et al*., 2005). Vit C is implicated in improving the eggshell quality by activating production of the active form of Vit D as well as enhancing the serum levels of Ca and P (Keshavarz, 1996; Sahin *et al*., 2002b). Moreover, Vit C is involved in collagen production during eggshell formation via its role in the hydroxylation of collagen substrates (proline and lysine) (Keshavarz, 1996). Vit E increases the serum concentrations of Ca, P, Zn and Mn (Sahin *et al*., 2001b; Sahin *et al*., 2002a, b) and protects the liver from oxidative damage induced by HS (Sahin *et al*., 2002b; Oral and Aktivite, 2008). Vit E may positively affect various functions of the liver, including production of the active form of Vit D, which is necessary for calcium metabolism and eggshell formation. Supplementing heat-stressed broiler breeders with 120 mg manganese proteinate/kg diet improved the eggshell thickness and eggshell strength (Zhu *et al*., 2015a,b,c) by improving the eggshell ultrastructure via the increased production of glycosaminoglycans and uronic acid, which are required for eggshell formation (Xiao *et al*., 2014).

Supplementation with 1.0 mg of brown marine algae per kg of diet enhanced the Haugh unit score in laying hens under HS conditions (Al-Harthi, 2014) because brown marine algae contain alginates with the ability to eliminate free radicals such as hydroxyl and superoxide radicals, thereby increasing the potential of the antioxidant defense system and suppressing lipid peroxidation (Zhu *et al*., 2015a,b,c). Supplementing the diet of laying hens with 2.0 g ethanol-extracted propolis/kg achieved better eggshell thickness compared with the control due to enhanced uptake of calcium and phosphorus (Seven, 2008) under HS conditions via improvements in nutrient digestibility and gut health (Olukosi and Dono, 2014). Propolis contains benzoic acid, 4-hydroxybenzoic acid and other compounds (Nina *et al*., 2015), which have acidic effects (Olukosi and Dono, 2014) as well as containing high levels of antioxidants, such as caffeic acid, ferulic acid, kaempferol and phenethyl caffeate (Kumazawa *et al*., 2004), which may protect the intestinal and shell gland from the oxidative damage induced by HS, thereby improving their functions. Supplementation with 50 mg gamma-aminobutyric acid/kg diet improved the eggshell strength in heat-stressed laying hens by enhancing the calcium and phosphorus available for eggshell formation (Zhang *et al*., 2012a,b; Zhu *et al*., 2015a,b,c) because the intestines were protected against oxidative damage due to the increased activities of antioxidant enzymes and decreased lipid peroxidation in the intestinal mucosa (Cheng *et al*., 2013), thereby enhancing the absorption of Ca and P under HS conditions (Chen *et al*., 2014).

These previous studies have demonstrated that improvements in egg quality were also accompanied by enhanced laying performance. However, supplementation with 400 mg epigallocatechin-3-gallate (Sahin *et al*., 2010), 50 g tomato powder (Sahin *et al*., 2011), or 0.4 g resveratrol/kg diet (Sahin *et al*., 2012a,b) increased egg production by improving the antioxidant defense system and inhibiting lipid peroxidation in heat-stressed quails, but the egg quality was not evaluated in these experiments. Thus, it is not clear whether powerful antioxidant nutritional factors that increase egg production under HS conditions can also improve the egg quality under the same conditions. Moreover, previous studies have indicated that nutritional factors can react with free radicals to detoxify them and inhibit lipid peroxidation, as well as positively affecting Ca and P utilization, thereby enhancing the production of normal quality eggs under high ambient temperature. However, not all nutritional factors with antioxidant properties have positive effects on Ca and P utilization when tested at high ambient temperatures. Thus, Fig. 2 shows the mechanisms that might be affected by nutritional factors to successfully obtain improvements in egg quality or egg production. However, further tests of their effects on egg quality could be helpful for improving our understanding of the mechanisms that underlie the effects of nutritional factors on enhanced egg quality.

Immunity: In poultry, the primary immune organs comprise the thymus, bursa of Fabricius and spleen, where immune cell production and differentiation and antibody production occur in these organs. HS causes oxidative damage to the cell membranes in immune organs (Xu *et al*., 2014; Xu and Tian, 2015); thus, Bartlett and Smith (2003), Niu *et al*. (2009a, b, c), Quinteiro-Filho *et al*. (2010), Liu *et al*. (2014) and Jahanian and Rasouli (2015) reported significant reductions in the relative weights of the immune organs due to HS, including the thymus, bursa and spleen, as well as decreases in the volume and lobule of thymic and lymphoid follicles and the medulla/cortex ratio (Tang and Chen, 2015). As a consequence of HS, Tang and Chen (2015) detected significant reductions in B and T lymphocytes, which led to decreases in the production of antibodies, changes in cytokine secretion and lower numbers of macrophages with reduced phagocytic ability (Mashaly *et al*., 2004; Xu and Tian, 2015; Ohtsu *et al*., 2015; Varasteh *et al*., 2015). These changes may explain why HS induces significant decreases in the antibody titers against Newcastle disease virus (NDV), infectious bursal disease virus (IBDV) and infectious bronchitis disease virus (IBV), as shown by Sohail *et al*. (2010) and Jahanian and Rasouli (2015).

Nutritional factors can overcome the negative effects of HS on the immune systems of poultry. Thus, supplementation with 0.3 or 0.4 mg selenium (Se)/kg diet improved the production of antibodies and macrophages and their phagocytic ability, as well as modulating the production of cytokines to a normal level by protecting lymphoid organs from oxidative damage via the suppression of lipid peroxidation due to enhanced antioxidant enzymes activities in these organs in heat-stressed broilers (Niu *et al*., 2009a; Xu *et al*., 2014; Xu and Tian, 2015). In addition, supplementation with 200 mg *Atractylodes macrocephala* Koidz polysaccharides (a traditional Chinese medicine) alone or with 0.3 mg Se per kg of feed modified the immune response of broilers to HS according to the same mechanism as Se (Xu *et al*., 2014; Xu and Tian, 2015), which indicates that *Atractylodes macrocephala* Koidz polysaccharides may have antioxidant properties. Supplementation with 0.6 mg Cr from inorganic or organic sources per kg of diet enhanced the antibody response by sheep red blood cells (Ghazi *et al*., 2012), while adding 0.8 or 1.0 mg organic Cr per kg of diet increased the antibody titers against NDV, IBV and influenza virus (Toghyani *et al*., 2007; Ebrahimzadeh *et al*., 2012; Jahanian and Rasouli, 2015). Cr may reduce the oxidative stress in immune cells caused by HS by enhancing antioxidants and decreasing lipid peroxidation (Roa *et al*., 2012) and Cr has positive effects on the relative weights of lymphoid organs and their functions (Ghazi *et al*., 2012; Jahanian and Rasouli, 2015). Supplementation with 300 mg Vit C alone or with 60 mg Zn per kg of diet significantly improved the antibody titers against NDV, IBDV and IBV due to increases in the weights of the lymphoid organs (Chand *et al*., 2014) as a consequence of protection from HS-induced injury by enhancing the antioxidant defense system and suppressing lipid peroxidation (Sahin *et al*., 2003a; Gursu *et al*., 2004; Panda *et al*., 2008). Dietary supplementation with 15000 IU Vit A or 200 mg Vit E per kg of feed increased the production of antibodies and macrophages, as well as their phagocytic ability (Niu *et al*., 2009bc), because Vit E and A are capable of reacting with ROS to suppress the oxidative damage induced by HS (Kucuk *et al*., 2003; Panda *et al*., 2008). Supplementation with 1.0% *Ligustrum lucidum* or *Schisandra chinensis* (Chinese herbal medicines) enhanced the antibody titer against NDV (Ma *et al*., 2005) by reducing oxidative damage to the immune organs and improving their cellular proliferation (Ma *et al*., 2005, 2007, 2009). The inclusion of 1.0 g of the probiotic *Bacillus licheniformis* per kg of feed, or 0.1% probiotic (commercial probiotic containing different species of bacteria) alone or with 0.5% mannan-oligosaccharides modulated the secretion of cytokines to a normal level and enhanced the NDV and IBDV antibody titers (Deng *et al*., 2012; Sohail *et al*., 2010) due to the inhibition of oxidative damage under HS conditions in broiler chickens (Sohail *et al*., 2011). In addition, the synthesis of antibodies was improved by adding 50 mg gamma-aminobutyric acid/kg feed, which protected immune cells from the over-production of ROS caused by HS due to the activation of the antioxidant defense system to normalize the ROS levels (Zhang *et al*., 2012a,b; Zhu *et al*., 2015a,b,c). Moreover, Tang and Chen (2015) detected significant improvements in the immune organs (thymus and bursa) as well as increases in B and T lymphocytes and normal production of cytokines in heat stressed-chickens treated with gamma-aminobutyric acid. Supplementation with 400 mg resveratrol/kg diet promoted the secretion of antioxidant enzymes (glutathione peroxidase, superoxide dismutase and catalase), prevented lipid peroxidation and obtained improvements in the relative weights of the immune organs (thymus, spleen and bursa) in chickens under HS conditions (Liu *et al*., 2014).

It is clear that nutritional factors with antioxidant properties can protect the immune organs (cell membranes of the immune organs) from the oxidative damage induced by HS, which increases the likelihood of successful vaccination as well as making heat stressed-chickens less susceptible to infection with various diseases, thereby improving public health and the growth performance of poultry. Nutritional factors can promote the production of antioxidant enzymes as well as reducing the lipid peroxidation and oxidative damage caused by HS but the mechanisms involved are unknown. In addition, most previous studies have focused on the effects of HS on the immune organs and their functions and how to ameliorate the negative effects of HS on the immune systems of chickens, although other avian species are more sensitive to HS and pathogens. Thus, further studies are required to elucidate the mechanisms that allow nutritional factors to reduce oxidative damage in chickens or other birds with greater sensitivity to HS.

Intestinal functions: HS causes changes in the intestinal morphology, where different intestinal segments (duodenum, jejunum and ileum) exhibit lesions that vary in their degree, as well as differences in their relative weight, villus height, villus surface area, crypt depth, immunoglobulin A-secreting cell area and epithelial cell area. In addition, the production of digestive enzymes (trypsin, chemotrypsin, amylase, maltase and sucrase) declines due to increases in ROS, which elevate lipid peroxidation of the intestine and pancreas cell walls, thereby negatively affecting nutrient digestion and absorption and positively affecting the sensitivity of the intestine to pathogens (Hai *et al*., 2000; Sahin and Kucuk, 2003; Burkholder *et al*., 2008; Gu *et al*., 2012; Cheng *et al*., 2013, 2015; Ma *et al*., 2014; Santos *et al*., 2015; Varasteh *et al*., 2015; Abdelqader and Al-Fataftah, 2016; Liu *et al*., 2016). In addition, HS can modify bacterial communities in the intestine by increasing the abundance of harmful bacteria (coliforms and *Clostridium*) and reducing that of beneficial bacteria (*Lactobacillus* and *Bifidobacterium*), which negatively affects gut health, digestion and nutrient absorption (Song *et al*., 2013, 2014; Al-Fataftah and Abdelqader, 2014; Abdelqader and Al-Fataftah, 2016). These changes may explain why HS decreases the productive performance, meat yield, egg yield, immune activity and the development of reproductive organs. In addition, these changes in bacterial abundance may explain why supplementation with various nutritional factors can eliminate ROS under HS conditions to improve the growth performance, meat, egg yield and quality. Supplementing the diet of heat-stressed chickens with 1.5 g probiotic (*Bacillus licheniformis*, *Bacillus subtilis* and *Lactobacillus plantarum*)/kg of feed improved the villus height and increased the abundance of beneficial bacteria, but reduced the amount of harmful bacteria (Song *et al*., 2014). In heat stressed-hens, supplementation with 1.0 g probiotic (*Bacillus licheniformis*)/kg of diet enhanced the villus height and IgA-secreting cell area (Deng *et al*., 2012). In broiler chickens exposed to HS, supplementation with 1.0 g probiotic (*Bacillus subtilis*)/kg of diet also improved the villus height, surface area, crypt deep and epithelial cell area, as well as increasing the counts of *Lactobacillus* and *Bifidobacterium*, but decreasing those of coliforms and *Clostridium* (Al-Fataftah and Abdelqader, 2014). Moreover, in heat stressed-chickens, supplementation with 1.0 g probiotic (*Lactobacillus*)/kg of feed enhanced the villus height and width, as well as the crypt depth, villus:crypt ratio and the surface area in different parts of the intestine (duodenum, jejunum and ileum) (Ashraf *et al*., 2013). In broiler chickens under HS conditions, supplementation with 1.5 g cello-oligosaccharide/kg of diet increased the villus height, villus:crypt ratio in the jejunum and the numbers of *Lactobacillus*, but decreased the numbers of coliforms (Song *et al*., 2013). In addition, supplementation with 5 g mannanoligosaccharides/kg of feed improved the villus height and width, crypt depth, as well as their surface area in the duodenum and ileum (Ashraf *et al*., 2013). In heat stressed-chickens, supplementation with 0.5 g butyric acid/kg of diet increased the relative weights of the intestinal segments, villus height, crypt depth, villus surface area and epithelial cell area, as well as the abundances of *Lactobacillus* and *Bifidobacterium* (Abdelqader and Al-Fataftah, 2016).

Dietary supplementation with probiotics, prebiotics (such as mannanoligosaccharides), or butyric acid can improve the intestinal morphology and populations of beneficial intestinal bacteria, as well as improving the productive performance of heat stressed-birds. Probiotics, prebiotics and butyric acid can improve the antioxidant defense system, decrease lipid peroxidation (Jahromi *et al*., 2015; Liao *et al*., 2015; Mishra *et al*., 2015; Shashidhara and Devegowda, 2003; Bozkurt *et al*., 2012; Zhang *et al*., 2011) and enhance populations of beneficial bacteria, thereby protecting against oxidative damage and allowing the intestine to develop normally. Thus, the inclusion of probiotics, prebiotics, or short chain fatty acids in the diets of heat-stressed birds can improve their intestinal morphology, thereby enhancing their productive performance, which may explain why several studies have detected improvements in productive performance when the diets of heat-stressed birds were supplemented with antioxidants. Thus, dietary supplementation with nutritional factors is recommended to protect meat, eggs and the immune system against the oxidative damage induced by HS in poultry. However, the effects of these nutritional supplements should be tested either alone or in combination with other probiotics or prebiotics to understand their effects on intestinal functions.

Fertility: Fertility is one of the most important traits that need to be evaluated in breeder flocks. In males, HS induces testicular injury by elevating testicular lipid peroxidation due to increases in ROS, which negatively affect the weight of testes, semen volume, sperm concentration, live and normal sperm count, spermatogonia, spermatocytes, spermatids, the positive dead sperm count and motility (Joshi *et al.*, 1980; Chen *et al.*, 2015; Türk *et al.*, 2015; 2016). McDanoiel *et al.* (1996) observed that the percentage of fertilized eggs decreased due to a decline in sperm-egg penetration when they inseminated hens with semen collected from heat-stressed roosters. However, nutritional factors that influence antioxidant properties may address the problem of low fertility under HS conditions. Thus, Ebeid (2009) attempted to alleviate the negative effects of high ambient temperature in roosters by dietary supplementation with different amounts of organic Se. It was shown that supplementation with 0.3 mg Se/kg of diet improved the number of live sperm and their mobility, as well as reducing the number of dead sperm by ameliorating the oxidative damage induced by HS in testicular tissues due to increases in the glutathione peroxidase levels and antioxidant capacity and by suppressing lipid peroxidation in seminal plasma. In addition, Ebeid (2012) successfully improved the number of live sperm and their mobility as well as reducing the number of dead sperm by supplementation with 200 mg Vit E/kg of diet alone or in combination with organic Se (0.3 mg/kg), which enhanced the antioxidant defense system and suppressed lipid peroxidation in the seminal plasma of heat-stressed roosters. In quails under HS conditions, supplementation with 250 mg cinnamon (*Cinnamomum zeylanicum*) bark oil or 125 mg rosemary oil per kg of diet as natural antioxidants enhanced the sperm count, spermatid count, spermatocytes and spermatogonia by protecting testicular tissues from oxidative damage via enhancement of the antioxidant capacity and inhibition of lipid peroxidation in testicular tissue (Turk *et al.*, 2015, 2016).

Dietary antioxidants are effective tools for improving male fertility in poultry under HS conditions but only a few antioxidants have been tested. Therefore, further studies are required to evaluate the effects of other antioxidants and their combinations on testicular functions and semen quality under HS conditions. In hens, HS induces oxidative damage to the small yellow follicles, ovary and oviduct, thereby significantly reducing the relative weights of the ovary and oviduct, oviduct length and the number of large follicles (Rozenboim *et al.*, 2007; Sahin *et al.*, 2009; Ma *et al.*, 2014; Cheng *et al.*, 2015). This may explain why HS significantly reduces egg production in avian species. Supplementation of heat-stressed poultry with nutrients that possess antioxidant properties supports this explanation (as described in our discussion of egg quality). Therefore, it is necessary to examine the effects of nutritional factors that improve egg production and egg quality on ovarian functions.

Conclusions: In poultry, HS has undesirable effects on the productive performance, meat quality, egg quality, immunity, intestinal functions and reproduction, but various nutritional factors can overcome these effects to reduce economic losses. Therefore, supplementation of heat-stressed poultry with nutrients at the levels recommended in previous studies can alleviate the deleterious effects of HS and improve the productive performance and the quality of meat and eggs (as well as semen). In addition, according to the effects of HS shown in Fig. 1-3, studies should be conducted to understand the effects of various nutritional factors in improving the meat quality, egg yield, egg quality, semen quality, immune system functions and intestinal functions in poultry under HS conditions.

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